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INTRASPECIFIC VARIATION IN SEED IMBIBITION OF BLACKBRUSH (*COLEOGYNE RAMOSISSIMA*: ROSACEAE).

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ABSTRACT

Intraspecific variation in blackbrush (*Coleogyne ramosissima* Torr.) seed imbibition was quantitatively investigated in the Mojave Desert. Blackbrush seeds were collected from six isolated mountain ranges, with each range sampled from one high-elevation (1550 m) and one low-elevation (1200 m) location for a total of 12 populations. Under laboratory experimental conditions, seed dry mass and initial seed moisture content did not differ significantly among the 12 populations. High-elevation source seeds imbibed significantly more water than low-elevation source seeds, and this was likely associated with habitat-specific selection. However, differences in full imbibition among seed collection sites at the identical elevation were not significant. Germination of field-collected seeds was similar, ranging from 87 to 93% among the 12 populations. Results of this study suggest that among six isolated mountain ranges in the Mojave Desert, blackbrush seed imbibition varies with elevation, but not with latitude.

Key Words: blackbrush, *Coleogyne ramosissima*, interspecific variation, Mojave Desert, seed imbibation.

Blackbrush (*Coleogyne ramosissima* Torr., Rosaceae) is often a dominant shrub species on shallow soils in the transition zone between North American warm Mojave Desert and cold Great Basin Desert (Bowns 1973; Bowns and West 1976; Meyer and Pendleton 2005). *Coleogyne ramosissima* is a mast-seeding species, producing abundant seed crops at intervals of a few to several years, with vegetative growth occurring at more frequent intervals (Pendleton and Meyer 2004). This species exhibits variation in seed dormancy (Lei 1997; Pendleton and Meyer 2004; Meyer and Pendleton 2005). Seeds collected from low-elevation sites are less dormant than seeds collected from high-elevation sites in southern Utah and Nevada (Lei 1997; Pendleton and Meyer 2004). *Coleogyne ramosissima* may also exhibit variation in the relative ability to imbibe water during germination. Such variation is often interpreted as a result of habitat-specific selection (Pendleton and Meyer 2004).

The objective of this study was to evaluate intraspecific differences in imbibition characteristics under controlled laboratory conditions for blackbrush seeds from various elevations and latitudes. I hypothesized that *C. ramosissima* seeds from different environmental conditions within the Mojave Desert would exhibit intraspecific variation in their relative ability to imbibe water.

From late June through early August 2005, *Coleogyne ramosissima* seeds were collected from six isolated mountain ranges in the Mojave Desert, with each range sampled from one high-elevation (1550 m) and one low-elevation (1200 m) location for a total of 12 populations (Table 1). The Spring Mountains, Newberry Mountains, and McCullough Range are located in southern Nevada; the Clark Mountain is located in southeastern California; the Mormon Range in southwestern Utah; and the Virgin Mountains in northwestern Arizona. An unusually large amount of rainfall occurred in late winter and early spring, and abundant seed crops were produced (Lei, personal observation). For this reason, no attempts were made to examine variation in full imbibition at the same or similar seed age.

A total of 2400 filled seeds were randomly collected from *C. ramosissima* shrubs and adjacent soil surfaces among the 12 populations. Because some seeds were collected from the soil surface the exact age of all seeds was difficult to determine.

All flattened, punctured, and wrinkled (damaged) seeds were discarded in the field. In the laboratory, full-sized but empty, inviable seeds were removed by floating off the unfilled fruits in water. Floating seeds were further examined for viability using a cut test, and empty seeds were discarded. To obtain maximum germination, filled seeds were stored at 4°C for six weeks in the dark (dry-chilling) prior to an imbibition experiment (Meyer and Pendleton 1990; Lei 1997).

Within each of the 12 populations, a total of 100 seeds were randomly selected, and placed in an oven, dried at 40°C for 36 hr to determine seed dry mass and initial moisture content. Seeds were weighed to the nearest 0.001 g with a digital

TABLE 1. SEED DRY MASS, INITIAL SEED MOISTURE CONTENT, IMBIBITION, AND OVERALL GERMINATION PERCENTAGE OF FILLED SEEDS FROM SIX ISOLATED MOUNTAIN RANGES IN THE MOJAVE DESERT. High-elevation sites were located at 1,550 m, and low-elevation sites were at 1200 m (n = 100 per elevation in each mountain range). Mean values other than germination percentages are expressed with standard errors.

Mountain range	Coordinates (*Lat.Long.*)	Elevation (*m*)	Seed mass (*mg*)	Moisture content (*%*)	Imbibition (*% wt. gain*)	Germination (*%*)
Clark Mountains, CA	35°21′N, 115°33′W	1200	22.7 ± 0.5	4.4 ± 0.1	17.8 ± 2.5	87
	35°41′N, 115°35′W	1550	21.6 ± 0.6	5.1 ± 0.2	22.4 ± 1.9	92
McCullough Range, NV	35°49′N, 115°11′W	1200	22.2 ± 0.5	4.9 ± 0.2	18.5 ± 2.3	88
	35°48′N, 115°09′W	1550	21.7 ± 0.4	5.6 ± 0.3	22.9 ± 1.7	90
Mormon Range, UT	37°05′N, 113°57′W	1200	21.4 ± 0.6	4.9 ± 0.2	18.6 ± 1.8	92
	37°04′N, 113°56′W	1550	21.5 ± 0.5	5.1 ± 0.2	21.9 ± 2.1	93
Newberry Mountains, NV	35°16′N, 114°42′W	1200	21.2 ± 0.6	4.8 ± 0.2	18.5 ± 1.5	92
	35°16′N, 114°43′W	1550	19.6 ± 0.4	5.3 ± 0.2	25.0 ± 2.0	93
Spring Mountains, NV	36°09′N, 115°44′W	1200	21.7 ± 0.6	5.0 ± 0.3	18.7 ± 1.9	90
	36°10′N, 115°42′W	1550	21.0 ± 0.5	5.1 ± 0.3	23.6 ± 2.7	88
Virgin Mountains, AZ	36°37′N, 114°09′W	1200	23.1 ± 0.6	4.9 ± 0.3	17.5 ± 2.7	91
	36°38′N, 114°08′W	1550	22.7 ± 0.6	5.0 ± 0.3	23.9 ± 2.1	89

balance scale (Ohaus Voyager PRO Precision Balance). Seed moisture content was computed using the following equation: (Fresh weight - dry weight/fresh weight) * 100 (Bewley and Black 1994). Seeds used for measuring initial moisture content were not used again for the imbibition experiment due to possible damage to embryos and/or endosperm tissues.

During the imbibition experiment, seven replications of 14–15 seeds were included in each population. Seeds were placed in 100-mm plastic Petri dishes between two moistened germination blotters. Seeds were incubated at 4° C in the dark for approximately 5 wk without light to decrease evaporative water loss, but were briefly exposed to soft-white fluorescent lights as seeds were pat-dried and weighed daily. Seeds were pat-dried with paper towels to remove free water on their seed coat before weighing. All 12 seed populations received 5 mL of water biweekly. Imbibition, the absorption of water by nonliving or senescent materials and subsequent swelling caused by adhesion of the water to internal surfaces of materials, is the initial step in seed germination (Bradford 1995; Jorgensen and Chesser 2000). At the end of the incubation period, all ungerminated seeds were examined for viability using a cut test. Germination percentage values were corrected for seed viability (Meyer and Pendleton 2005).

Germination percentage of filled seeds in each of the 12 populations was computed. Two-way Analysis of Variance (Analytical Software 1994) was performed on seed dry mass, initial seed moisture content, and mass at full imbibition (i.e., percent gain in mass), with elevation and latitude as main effects. Pearson's correlation (Analytical Software 1994) was conducted to correlate seed germination percentage with water content at full imbibition. Mean values and standard errors were calculated, and statistical significance was determined at $P \leq 0.05$.

Across the Mojave Desert, it is common for *C. ramosissima* seeds to reach full size but fail to fill. Unfilled and/or damaged seeds ranged from 32% in the Virgin Mountains to 44% in the Spring Mountains, with both extreme percentages occurring at the low-elevation sites.

Nevertheless, seed dry mass and initial seed moisture content did not differ significantly among six latitudes or between high and low elevation (ANOVA, $F_{11,1188} < 1.02$, $P > 0.05$; Table 1). The elevation * latitude interaction was also not statistically significant for seed dry mass (ANOVA, $F_{11,1188} = 1.00$, $P > 0.05$) and initial seed moisture content (ANOVA, $F_{11,1188} = 0.44$, $P = 0.5551$; Table 1), indicating that these two traits were similar among the 12 seed populations.

Seeds gain some mass immediately upon wetting among filled seeds. Seeds imbibed water at a similar rate regardless of collection site. The greatest imbibition occurred during the first four days, and then increased slowly with slight oscillations. Seeds generally reached a maximum imbibition weight after 12 d. Differences in water content at full imbibition did not affect the timing of germination. No consistent pattern was found between differences in imbibition and the timing of germination. Germination of most seeds was observed within 2–3 wk of the initial experiment, and germination occurred within a few days after full imbibition regardless of collection site.

Coleogyne ramosissima seeds collected from high-elevation sites imbibed significantly more water (ANOVA, $F_{11,1188} = 56.17$, $P \leq 0.0001$; Table 1) compared to seeds collected from low-elevation sites. However, differences in water content at full imbibition among latitudes at the same elevation were not statistically significant (ANOVA, $F_{11,1188} = 0.59$, $P = 0.7071$; Table 1).

Similarly, the elevation * latitude interaction was not statistically significant (ANOVA, $F_{11,1188}$ = 1.02, P = 0.4531; Table 1), indicating that water content at full imbibition was similar in all 12 seed populations at similar elevations.

The overall germination percentages were similar among the 12 populations, ranging from 87% at the low-elevation site in the Clark Mountain to 93% at the high-elevation site in the Mormon Range. Correlation between germination percentage of filled seeds and water content at full imbibition was positive and highly significant (df = 10, r = 0.88, P ≤ 0.001).

The direction of selection on *C. ramosissima* seed imbibition trait may depend on local environmental conditions. My data indicate that imbibition of seeds varies as a function of elevation among populations. This variation suggests selection for seed imbibition in response to climate and differences in maternal environmental conditions.

However, no latitudinal variation in imbibition was found in this study. The lack of significant variation at the identical elevation in spatially separated mountain ranges may not reflect past selection for latitudinal differences within the relative small (geographically restricted) Mojave Desert.

Results of this study indicate the existence of habitat-correlated variation in seed imbibition response for *C. ramosissima*. Intraspecific variation in seed imbibition was found, a threshold trait, between two distinct elevations under controlled laboratory conditions. Seeds collected from low-elevation sites imbibed significantly less water, whereas seeds collected from high-elevation sites imbibed more water during the imbibition experiment. Since maternal plants were growing under different environmental conditions, these differences may be due to habitat-specific selection. Variation in *C. ramosissima* seed imbibition was probably a result of evolutionary fine-tuning in response to variation in local environmental regimes. In these mountain ranges, moisture availability changes with elevation and may have selected for the observed differences in seed imbibition between higher and lower elevations.

Although the ecological consequences of differences in imbibition in general or for other plant species remain poorly understood, *C. ramosissima* seeds collected from low-elevation sites have responded to soil moisture limitation by imbibing less water than seeds collected from high-elevation sites. Due to a predictable hot and dry environment at low elevations, selection should favor seeds that imbibe less water prior to germination compared to high elevations in the Mojave Desert.

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Literature Cited

Analytical Software. 1994. Statistics 4.1, an interactive statistical program for microcomputers. Analytical Software, St. Paul, MN.

Bewley, J. D. and M. Black. 1994. Seeds: physiology of development and germination. Plenum Press, New York, NY.

Bowns, J. E. 1973. An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in Southwestern Utah. Doctoral dissertation, Utah State University, Logan, UT.

——— and N. E. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southern Utah rangelands. Utah Agricultural experimental Station, Research Report 27. Department of Range Science, Utah State University, Logan, UT.

Bradford, K. J. 1995. Water relations in seed germination. Pp. 351–396 *in* J. Kigel and G. Galili (eds.), Seed development and germination. Marcel Dekker, New York, NY.

Jorgensen, E. E. and K. L. Chesser. 2000. Intraspecific differences in grass seed imbibition. Western North American Naturalist 60:433–438.

Lei, S. A. 1997. Variation in germination response to temperature and water availability in blackbrush (*Coleogyne ramosissima*) and its ecological significance. Great Basin Naturalist 57:172–177.

Meyer, S. E. and B. K. Pendleton. 2005. Factors affecting seed germination and seedling establishment of a long-lived desert shrub (*Coleogyne ramosissima*: Rosaceae). Plant Ecology 178:171–187.

——— and R. L. Pendleton. 1990. Seed germination biology of spinless hopsage: between population differences in dormancy and response to temperature. Pp. 187–192 *in* McArthur, E. D., E. M. Romney, S. D. Smith, and P. T. Tuller (comps.) Proceedings–symposium on cheatgreass invasion, shrub die-off, and other aspects of shrub biology and management. Las Vegas, NV, April 5–7, 1989.

Pendleton, B. K. and S. E. Meyer. 2004. Habitat-correlated variation in blackbrush (*Coleogyne ramosissima*: Rosaceae) seed germination response. Journal of Arid Environments 59:229–243.